Characteristics and distribution of intermediates between Platanthera bifolia and P. chlorantha (Orchidaceae) in the Nordic countries

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In areas of sympatry *Plantanthera bifolia* (L.) L. C. Rich. and *P. chlorantha* (Cust.) Rchb. occasionally produce hybrids. These plants exhibit intermediate floral morphology. The present study presents the distribution, floral morphology, and general characteristics of these intermediates in the Nordic area. The most useful and reliable diagnostic characters for hybrid plants were (1) the distance between viscidia (normally about 1.4 mm), (2) the length of the caudicle of pollinia (about 0.7 mm), and (3) the presence of a distinct pedicel at the connection between caudicle and viscidium. Comparative chemical analyses of the floral fragrances are reported.
Material in the principal Nordic herbaria indicated a generally low production of hybrids (0.46%) and that the main area of occurrence is SE Sweden and Alandia, Finland. Intermediates seem more frequent in provinces where *P. bifolia* is relatively long-spurred. Very few were recorded from Denmark and Norway (hybrids in the latter country here reported for the first time). Aggregations of intermediates displaying patterns of introgressive hybridization were found only on Öland and Gotland. Occurrence of hybrids outside the Nordic area is also discussed and remarks are made on the morphologically similar *P. metabifolia* Maek. in E Asia. All known Nordic intermediates are listed.

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Introduction

The occurrence of intrageneric *Platanthera* hybrids is a well-documented phenomenon both in the Nearctic and Palaearctic region (e.g. Müller 1868, Hardin 1961, Stoutamire 1974, Inoue 1983a). Two disparate specializations in the deposition of pollinaria on pollinating Lepidoptera, viz. proboscis- and eye-attachment, are wide-spread in the genus and sympatric species-pairs displaying these specializations often occur (Nilsson 1981). Because of the small delimited firm surfaces on moths' heads favourable for attachment of viscidia, hybrid plant individuals with intermediate column morphology are predicted to have a strongly reduced male fitness.

Species isolation between the Eurasian orchids *Platanthera bifolia* (L.) L.C. Rich. and *P. chlorantha* (Cust.) Rchb. involves a set of exclusively external mechanisms – mechanical, ethological, and seasonal (Nilsson 1983). These species are fully infertile and interspecific pollen transfer occasionally occurs by pollinating moths. In most areas of sympatry, single records of intermediate plants indicative of hybridization have been reported. Small swarms of such individuals are temporarily produced at least in certain areas in W Europe, for example on the islands of Öland and Gotland in the Baltic. Intermediates face considerable difficulties in dispersing their male gene-material on pollen vecting moths and thus function merely as additional female recipients in the *Platanthera* populations. Since

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they also are less pollinated, the hybrids tend to become eliminated by natural selection while their offspring are involved in occasional patterns of introgressive hybridization.

The hybrids and backcross individuals exhibit various intermediate features between the two parental species. As pointed out by Hylander (1966), this situation has led to consistent problems how to interpret and identify the actual plant material both in the Nordic area and elsewhere, and a closer study is required to solve the matter. The functional aspects of the intermediates and details of hybridization were recently presented (Nilsson 1983). The aim of the present paper is to clarify how products of hybridization between *P. bifolia* and *P. chlorantha* can be discovered and identified in the field and in museum collections. Particular reference will also be made to the frequency and geographic distribution of hybrids in NW Europe.

Material and methods

Intermediates between *P. bifolia* and *P. chlorantha* were studied in the field on Öland and Gotland, Sweden. Measurements were carried out on one randomly selected flower per inflorescence, avoiding top and bottom positions. Two pollinaria from each plant individual were collected by attaching their viscidia onto a small piece of plastic and later studied in a binocular stereomicroscope.

Collection of floral fragrance compounds in typical individuals of *P. bifolia, P. chlorantha* and F_1-hybrids from central Öland was made by a slightly modified precolumn sorption technique (Bergström et al. 1980). The tube with packed active sorption agent Porapak Q was extracted with pentane and chemical analysis of the concentrated extract was carried out by gas chromatography (GC) and combined gas chromatography – mass spectrometry (GC-MS). In a quantitative analysis, fragrance was collected from one inflorescence of each category of plant with 20 open flowers during three hours in the night (22.00–01.00).

Since intermediate plants in the herbaria were most often discovered among material labelled either *P. bifolia* or *P. chlorantha,* all material of these species and those labelled as hybrids in the principal Nordic herbaria were investigated: AAU, BG, C, GB, H, KUO, LD, O, OULU, S, TRH, TROM, TUR, UME, and UPS. In addition, material deposited as hybrids and as *P. bifolia* and *P. chlorantha* from Asia in the following herbaria was examined: BM, G, K, M, and W. One flower with at least one pollinarium left was heated in water and dissected as soon as a specimen showed signs of being intermediate or was otherwise questionable concerning its identity. All material used in the course of the present study, and the identity of it, has been indicated by small labels with the present author's name, attached to each herbarium sheet.

Results and discussion

Morphology

General. The two species are vegetatively virtually identical. The fundamental differences in floral morphology in relation to pollinating moths (Darwin 1862, Nilsson 1983), make hybrids and their derivatives readily detectable by close examination of floral structures. In overall view, the floral morphology in hybrid plants is intermediate (Fig. 1). The sepals are normally broader than in *P. bifolia.* The petals are often overarching the column, but not as close as in *P. chlorantha* (Fig. 2). The length of the spur in intermediates is usually 20–30 mm (Fig. 3, bottom). On Öland, where hybridization involves a very long-spurred *P. bifolia* race, the spur-length is frequently over 30 mm (Tab. 1). The latter measurements indicate that hybrids develop spur-lengths most frequently around the mean of the means of the two parental populations in an area. In *P. chlorantha,* the spur is usually a little expanded towards the tip, and thicker than in *P. bifolia.* Also hybrids often exhibit somewhat expanded spurs. Nectar secretion is abundant, and probably quantitatively intermediate in hybrid plants (Nilsson 1983).

Column. Only close examination of the column, including the pollinaria, can state if a plant is hybridogenous. In hybrids, the column is larger than in *P. bifolia* and much smaller than in *P. chlorantha* (Fig. 2). The two pollination specializations, attachment of the pollinaria onto proboscis-base or compound eyes, respectively, are morphologically expressed in two sets of species-specific features. Functionally crucial is that the viscidia are close in *P. bifolia* and far apart in *P. chlorantha*

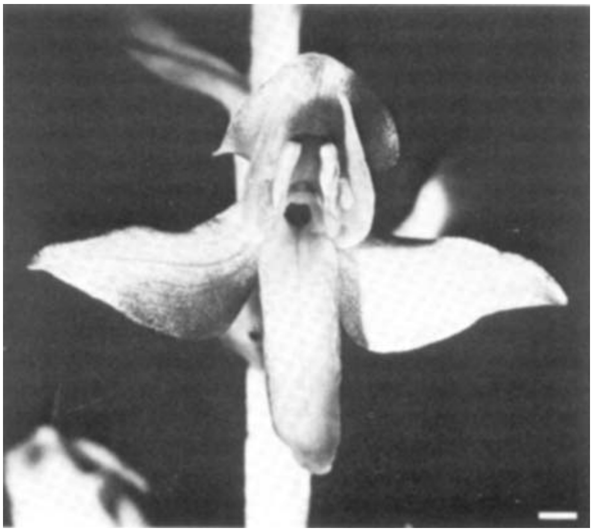


Fig. 1. Flower of a typical intermediate between *Platanthera bifolia* and *P. chlorantha*. – Scale: 1 mm.

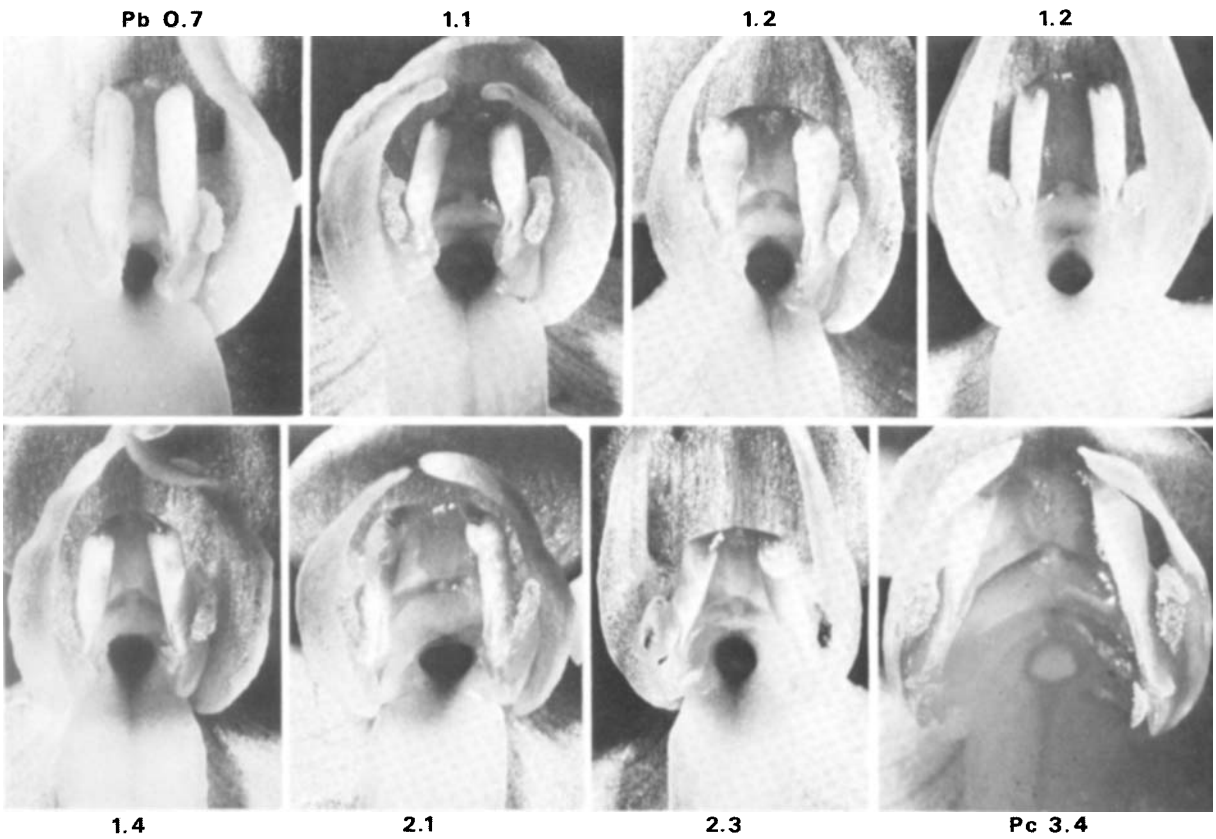


Fig. 2. Column of *Platanthera bifolia* (Pb) and *P. chlorantha* (Pc), and a series of intermediates. The distance between viscidia in the intermediate columns is indicated (in mm).

(Tab. 1). Hybrids and backcrosses exhibit distances between the viscidia between those of the two species (Nilsson 1983: Fig. 7). Measurements of fresh material from Öland and Gotland indicate that F_1-plants have a distance between the viscidia of about 1.4 mm ($\bar{x}$ = 1.41, SD = 0.44, n = 126), which is intermediate, but not around the mean between the distance in the two parental species (Tab. 1). In consequence, the lateral column structures which support the viscidia show principal differences (Fig. 4). In *P. chlorantha* the flanks are elongate and project far beyond the spur-mouth and above the labellum surface, a character normally easy to observe also in pressed material. In *P. bifolia* the flanks are subtruncate, not projecting. Hybrids and backcrosses normally have distinctly protruding flanks of the column and are thus intermediate (Fig. 4). The connective in hybridogenous plants is intermediate but a rather strong variability exist both in breadth and height, and thus also in the angle of the anther loci (Fig. 2).

The form of the stigma differs also between the two species. In *P. bifolia* the two lateral lobes are the largest and form two massulae-collecting "knobs" in front of the spur-mouth. The median lobe is small. In *P. chlorantha* the median lobe is the largest but also the two lateral lobes are well developed, together forming a very large sticky surface. Hybrid plants have intermediate

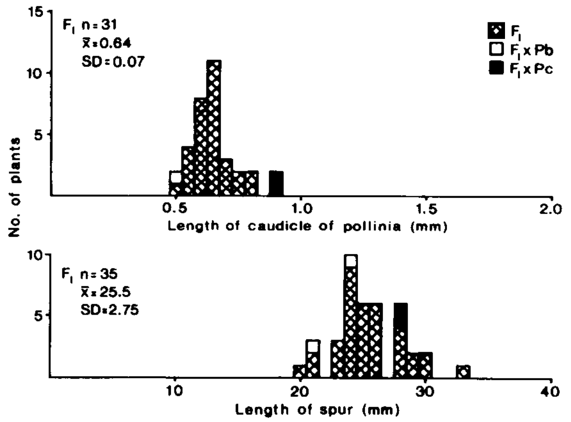


Fig. 3. Length of caudicle of pollinia and length of spur in intermediates between *Platanthera bifolia* and *P. chlorantha*. Data from material in the principal herbaria of the Nordic countries.

Tab. 1. Morphometry of selected characters in *Platanthera bifolia* (Pb), *P. chlorantha* (Pc), and intermediates (Pb × Pc). On Öland, measurements are only given for the extremely long-spurred race of *P. bifolia*, the one predominantly involved in hybridization. For how the length of the caudicle of pollinia was measured, see Fig. 6 J,S. When letters at mean-values differ, data on intermediates are differing by $P < 0.05$ (t-test) vs. *P. bifolia* and *P. chlorantha*.

	Öland				Gotland			
	n	$\bar{x}$	SD	Range	n	$\bar{x}$	SD	Range
Length of spur (mm)								
Pb	336	38.3[b]	4.40	26–52	313	31.9[a]	3.67	23.0–42.5
Pb × Pc	89	30.8[a]	3.84	21–39	9	29.6[a]	2.47	26.5–33.5
Pc	202	25.0[c]	2.94	18–32	52	32.9[b]	4.07	24.0–42.5
Distance between viscidia (mm)								
Pb	168	0.69[b]	0.18	0.3–1.2	40	0.73[b]	0.16	0.3–1.1
Pb × Pc	91	1.38[a]	0.43	0.7–2.3*	26	1.48[a]	0.48	0.8–2.6
Pc	117	3.43[c]	0.44	2.5–4.8	128	3.70[c]	0.49	2.2–4.9
Length of caudicle of pollinia (mm)								
Pb	149	0.33[b]	0.07	0.20–0.55	31	0.29[b]	0.06	0.19–0.42
Pb × Pc	72	0.68[a]	0.15	0.40–1.10	7	0.74[a]	0.25	0.40–1.08
Pc	121	1.70[c]	0.18	1.25–2.20	12	1.38[c]	0.18	1.08–1.71
Length of viscidium (mm)								
Pb	123	0.63[a]	0.07	0.48–0.89	31	0.60[a]	0.07	0.49–0.77
Pb × Pc	34	0.64[a]	0.06	0.55–0.78	7	0.64[a]	0.06	0.54–0.73
Pc	33	0.79[b]	0.06	0.69–0.94	12	0.76[b]	0.06	0.68–0.89
Breadth of viscidium (mm)								
Pb	123	0.49[b]	0.05	0.36–0.62	31	0.46[b]	0.06	0.36–0.59
Pb × Pc	34	0.58[a]	0.05	0.50–0.68	7	0.59[a]	0.05	0.49–0.66
Pc	33	0.70[c]	0.06	0.59–0.84	12	0.68[c]	0.07	0.54–0.81
Breadth/length ratio of viscidium								
Pb	123	0.78[b]	0.07	0.63–0.98	31	0.77[b]	0.06	0.65–0.89
Pb × Pc	34	0.91[a]	0.06	0.79–1	7	0.92[a]	0.04	0.79–0.98
Pc	33	0.88[c]	0.05	0.81–1	12	0.89[a]	0.07	0.76–0.99

*A single aberrant specimen had the distance 3.1 mm.

stigmas with normally subequal lobes (cf. Nilsson 1983: Fig. 3).

Viscidia. In the intermediates, viscidia are, on average, larger than in *P. bifolia* and smaller than in *P. chlorantha* (Fig. 5). The breadth tends to lie between that of the two species (Tab. 1). In *P. bifolia,* the viscidia are normally distinctly longer than broad (Fig. 6 T), the breadth/length ratio normally falling in the interval 0.70–0.90. In *P. chlorantha,* the viscidia are more suborbicular (Fig. 6 Y,Z) and the ratio frequenly 0.85–0.95. The viscidia in intermediates tend to be even more suborbicular in shape (Tab. 1; Fig. 6 U–X; Fig. 5). The surface of the viscidia is smooth in *P. chlorantha* (outside the pedicel) but in *P. bifolia* the surface usually exhibits one or more minute ridges after the viscidia have dried on a pollen vector (Fig. 6 T). These ridges result from desiccation of hygroscopic tissue on the disc that operates in the movement of the pollinaria on the moth's proboscis shortly after the pollinaria have been removed from the flower (Darwin 1862). Intermediates exhibit either distinct or indistinct ridges on the disc (cf. Fig. 6 U–X).

The point where each caudicle is connected to the viscidium is distinctly displaced from the centre in *P. bifolia,* the distance to the front margin often being only half that to the hind margin (Fig. 6 T). On the column, this point is situated in the upper outer part of each viscidium (Nilsson 1983: Fig. 3). In *P. chlorantha* the place of the caudicle attachment is more central (Fig. 6 Y,Z), and normally situated in the upper inner portion of the viscidium. In intermediates the caudicle attachment is regularly subcentral on the disc (Fig. 6 U–X).

The direction of the length-axis of the viscidia on the column is forward-upward in *P. bifolia,* but backward-upward in *P. chlorantha.* In intermediates the direction is indistinct. Consequently, both the somewhat differing shape of viscidia and position of the caudicle attachment in the intermediates are in fact intermediate features produced by suppression of two extremes.

Pedicel (stipes). This structure, a hygroscopically active mass of cells connecting the caudicle with the viscidium, is well developed in *P. chlorantha* (Fig. 6 P–S, Y,Z). In this species, the pedicel rotates the pollinium into a position suitable for striking a stigma shortly after the pollinarium has been removed, attached onto the pollinator's eyes (Darwin 1862). There is no pedicel in *P. bifolia* in N Europe. It is reduced but still distinct in hybrids and putative 1st backcross individuals (Fig. 6

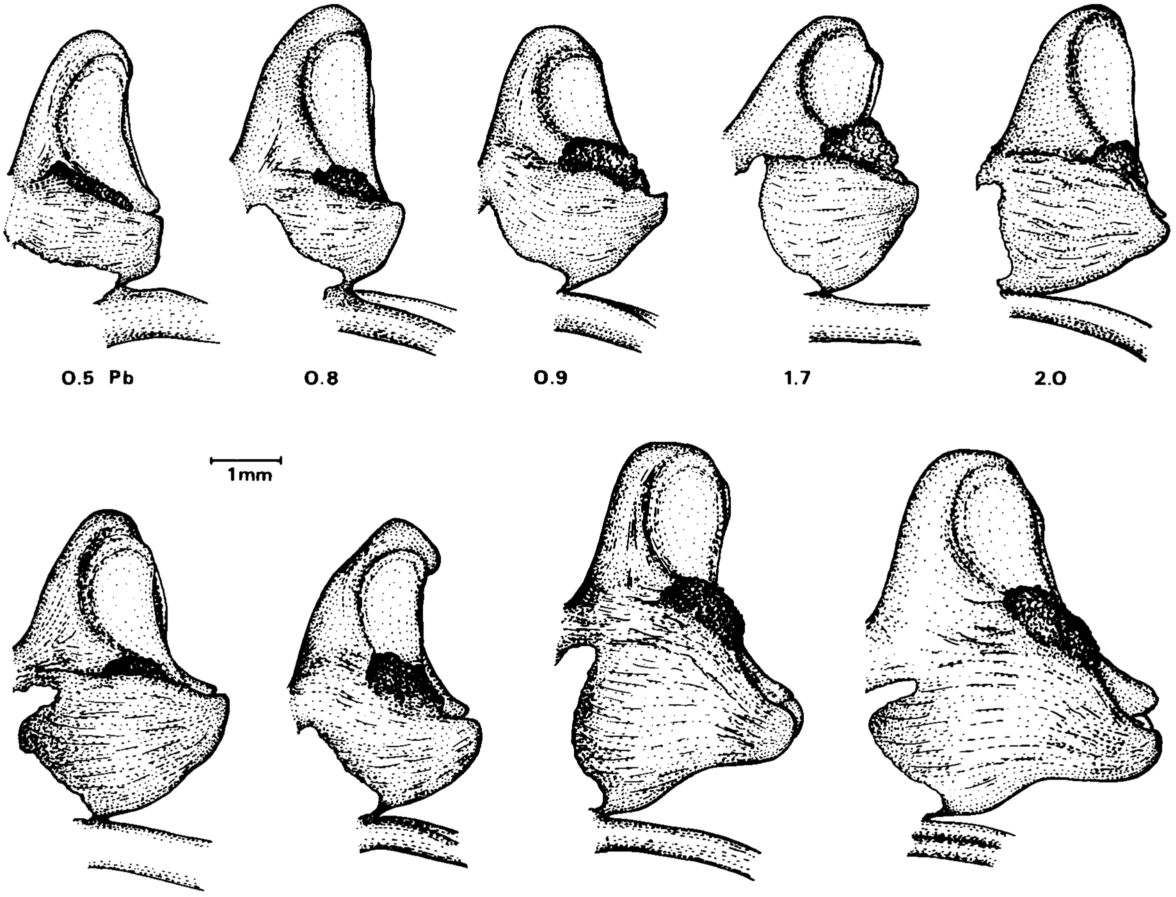


Fig. 4. Lateral view of column in *Platanthera bifolia* (Pb) and *P. chlorantha* (Pc), and a series of intermediates. The distance between viscidia of the illustrated columns is indicated (in mm).

B–O). This is a very useful character for detection of intermediates.

Caudicle. As a result of the two pollination systems a principal difference exists in the dimensions and structure of the caudicle of pollinia between *P. bifolia* and *P. chlorantha* (Fig, 6 A,Y,Z). In *P. bifolia* the caudicles are short, usually 0.2–0.4 mm, while in *P. chlorantha* they are much longer, usually 1.4–2.0 mm (Tab. 1). Both material from Öland and Gotland and the herbarium material indicate that the length in F_1-hybrids normally is 0.55–0.8 mm (Fig. 3, top). In *P. chlorantha* the caudicles are much more robust since they are specialized organs which carry pollinia beyond the face of the pollen vector (Nilsson 1978). Hybrids still display strong lateral borders and a rigid structure of the caudicle. The proximal tip of the caudicle is elongated and conspicuous in *P. chlorantha,* and more or less distinct also in intermediates, while in *P. bifolia* it is minute or virtually absent (Fig. 6 A).

Pollinia. In *P. chlorantha* the pollinia are club-shaped while those in *P. bifolia* are crescent-shaped. Hybrids show intermediate form (Nilsson 1983: Fig. 4). The massulae are rather loosely arranged in *P. bifolia* and thus the pollinia are distinctly more friable than in *P. chlorantha.* Also in this respect hybrids are intermediate.

Fourteen important or useful diagnostic features including those mentioned in the preceding paragraphs have been summarized in Tab. 2. To state if a plant individual is a hybrid, or a backcross, the characters Nos. 7, 10, and 13 have to be investigated in the first place. There was a strong positive correlation between characters No. 7 (distance between viscidia) and No. 13 (length of caudicle) in intermediate plants on Öland (r = 0.631; $t_s = 6.606$, df = 66, $P \leqslant 0.001$). Dissected columns of herbarium specimens indicated that this would certainly hold true also in other areas in W Europe.

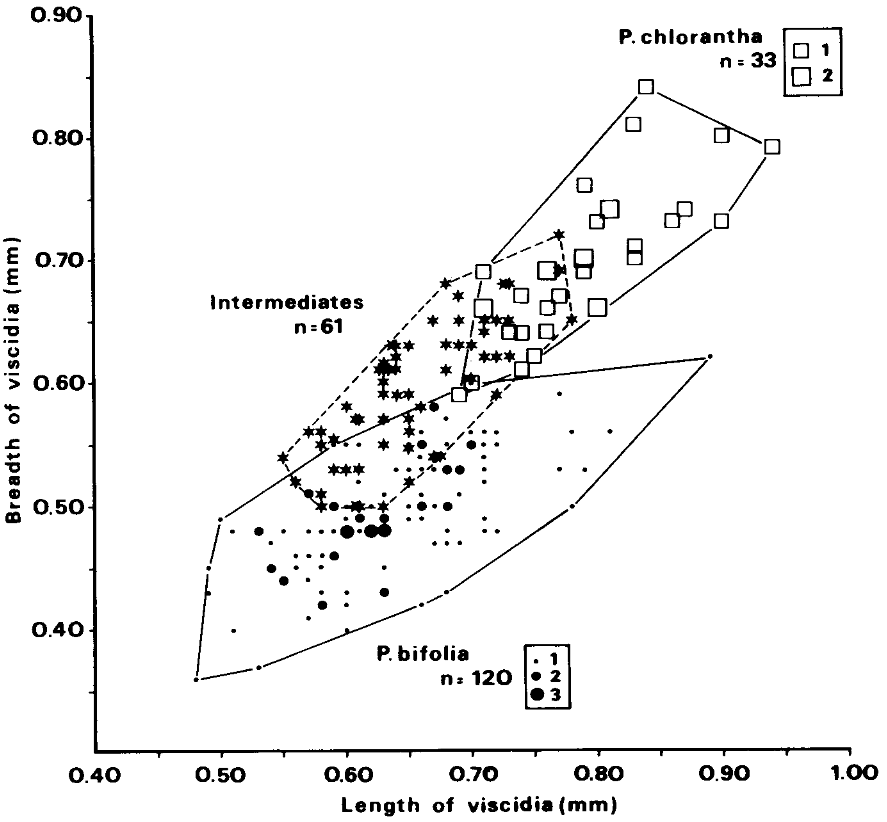


Fig. 5. Breadth and length of viscidia in *Platanthera bifolia*, *P. chlorantha*, and intermediates. Based on material from Öland. Data on *P. bifolia* represent the long-spurred race.

Anthesis

On Öland and Gotland the long-spurred *P. bifolia* races commence flowering more than two weeks earlier than *P. chlorantha*. Anthesis in hybrids was observed to be distinctly intermediate between the two species. Often hybrid individuals could be located even at a distance because of their slightly deviating stage of anthesis.

Floral fragrance

The chemical analyses revealed the floral fragrances of *P. bifolia* and *P. chlorantha* to be principally different (Tab. 3). Aromatic esters made up about 66% of the fragrance in *P. bifolia,* but only 29% in *P. chlorantha.* Linalool and geraniol together made up 25% in *P. bifolia,* but were not found at all in *P. chlorantha*. A series of lilac alcohols dominated (68%) in *P. chlorantha* while these compounds were totally absent in *P. bifolia*. GC indicated that both plants emit large quantities of fragrance compounds, contrary to human perception which experiences *P. bifolia* as being much more odoriferous.

Hybrids emitted a blend of the parental fragrance constituents, and at much lower rate (*vide* also Nilsson 1983). About 17 and 9 times less methyl benzoate were emitted compared to typical *P. bifolia* and *P. chlorantha,* respectively. The production of lilac alcohols was about 10 times less than in *P. chlorantha.* To humans, the hybrids are normally experienced as rather strongly scented, although less than *P. bifolia.* This is probably due to the large number of compounds, especially aromatics. A few compounds are obviously produced more by the hybrid than by either parent, e.g. geranial, neral, nerol, and benzyl alcohol. In addition to the periodically emitted compounds, which during the active period in the evening made up over 90% of the fragrance in all three categories of plants, there was a continuous unperiodic emission of terpene hydrocarbons mainly from the vegetative parts.

Distribution in the Nordic area

General occurrence. A total of 39 intermediates (hybrids and distinct backcross individuals) were present in the collections of the Nordic herbaria (Tab. 4; listed in Appendix). The major part (69%) originated from Sweden while very small numbers were recorded from Norway, Finland, and Denmark. The area of main distribution was the SE part of Sweden and Alandia, Finland (Fig. 7). The relative occurrence of intermediates was low in all provinces. Since 78% of the Scandinavian

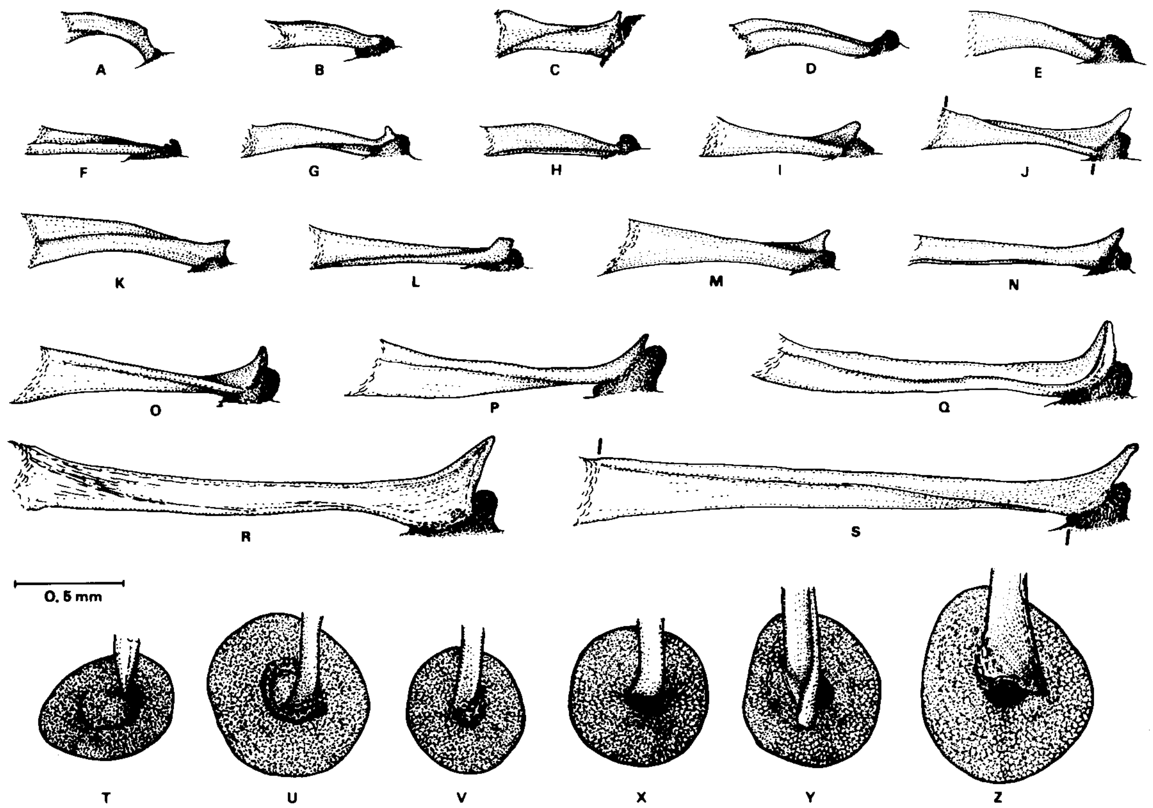


Fig. 6. Caudicle, pedicel, and viscidia in *Platanthera bifolia* (A,T) and *P. chlorantha* (P–S, Y,Z), and intermediates (B–O, U–X). Note the distinct pedicel in intermediates. Intermediates D–I were interpreted as F_1-plants, and B,C, J–O as putative backcrosses. The caudicle of C represents an aberrant and rare type. The marks in J and S indicate how length of caudicle of pollinia was measured.

herbarium material originally determined as hybrids (n = 64) by various botanists was misidentified (they were either *P. bifolia* or *P. chlorantha*), records from the literature, or elsewhere, not verified by voucher specimens, have been excluded in the present study.

Hybrid swarms. The museum collections gave no clear indication of presence of hybrid swarms in the Nordic area. Since three individuals, of which one is a putative backcross, were recorded from Omberg, Östergötland, temporary aggregations are perhaps produced on that locality. In the field, aggregations of *Platanthera* intermediates were found in some places on central Öland and in one locality on Gotland (see Appendix). Although probably more common than indicated in the herbaria, hybrid swarms in the Nordic area must be of rare occurrence. Hylander (1966) wrote that in some places virtually all plants show intermediate characters, having in mind the report from two islands in Blekinge by Erikson (1918). However, all plants collected by Erikson and others from these places, now in herbaria, were all definite *P. chlorantha*.

Introgressive hybridization. The isolated backcross plants suggest, although being very rare, the possibility of a low degree of interspecific gene-exchange in areas of sympatry. In the small hybrid swarms mentioned on Öland and Gotland, introgressive patterns were found, viz. mainly into *P. bifolia* on Öland but in both directions on Gotland (Nilsson 1983).

Factors affecting distribution. In addition to interactions between pollinating moths and *P. bifolia, P. chlorantha,* and intermediates described previously (Nilsson 1983), some further aspects have been tested. There is no significant correlation (at the 5% level) between the number of intermediates (Tab. 4) and the number of collected *P. bifolia* or *P. chlorantha* plants (a rough estimate of "abundance") in the provinces (Tab. 5). The number of intermediates versus the difference in this "abundance" between the species has a rather high negative correlation coefficient i.e. perhaps when *P. chlorantha* is more abundant than *P. bifolia* the numbers of intermediates produced are somewhat higher.

The number of hybrids is negatively correlated with

Tab. 2. Features of *Platanthera bifolia*, *P. chlorantha*, and intermediates (including F_1-hybrids and putative 1st backcrosses) in the Nordic countries. The most useful diagnostic characters are indicated by bold letters.

Character	*P. bifolia*	Intermediates	*P. chlorantha*
1. Floral fragrance	Very strong, mainly aromatic esters	Strong to weak, blend	Weak but distinct, mainly lilac alcohols
2. Lateral petals	Erect	Suberect to overarching	Overarching
3. Spur	Filiform, seldom expanded towards tip, 7–52 mm	Filiform to thick, often somewhat expanded towards tip, 20–39 mm	Normally thick and expanded towards tip, 17–45 mm
4. Connective	Narrow, normally <1 mm	Broad to rather narrow	Broad, often >2 mm
5. Flanks of column	Small, subtruncate	Rather large, protruding	Large, protruding
6. Anther loci	Subparallel	Angled to parallel	Angled
7. **Distance between viscidia**	Small: 0.3–**0.7**–1.2 mm	Normally: 1–**1.4**–2 mm	Long: 2.2–**3.5**–4.9 mm
8. Shape of viscidia	Normally distinctly longer than broad	Suborbicular	Suborbicular
9. Ridges on viscidia	Normally distinct	Often indistinct	Absent
10. **Pedicel (stipes)**	**Absent**	**Distinct**	**Distinct, large, rounded**
11. Caudicle-attachment on viscidia	Distinctly more towards upper outer portion	Subcentral	Normally somewhat towards upper inner portion
12. Proximal tip of caudicle	Very small or absent	Normally distinct	Distinct, well developed
13. **Length of caudicles**	Short: 0.2–**0.3**–0.5 mm	Normally: 0.5–**0.7**–0.9 mm	Long: 1.1–**1.7**–2.2 mm
14. Stigma lobes	Two lateral strongly developed, median smaller	Subequal	Median largest, two lateral rather large

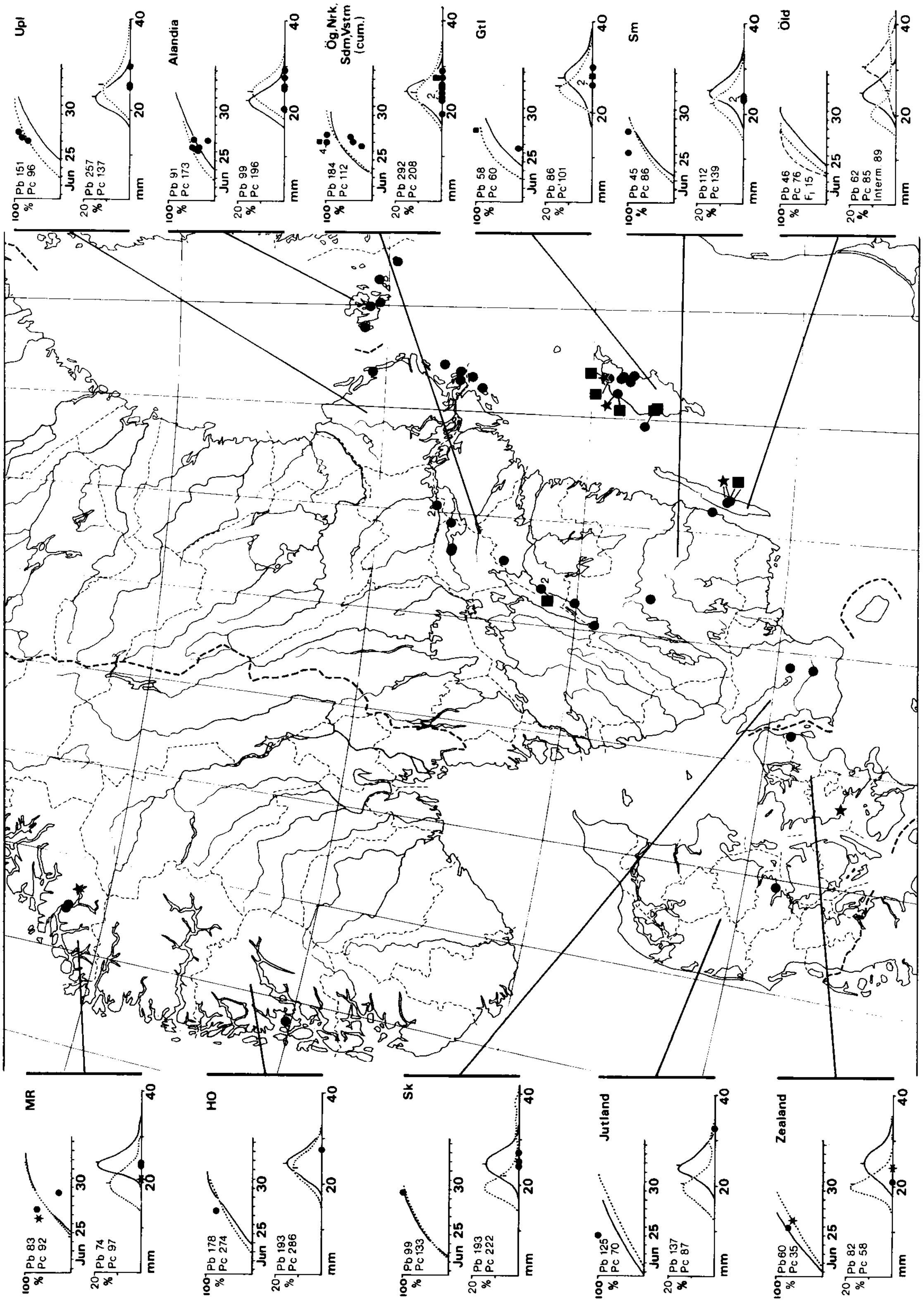
the spur-length in *P. chlorantha,* but shows no correlation with that in *P. bifolia,* or with the provincial difference in spur-length between the two species (Tab. 5). There is no correlation between the number of hybrids and the separation in days between the mean dates of 50% anthesis of the parental species.

Although hybrids usually exhibit spur-lengths around the mean between the means of the parental populations (see above), the intermediate individuals in the herbarium material had spur-lengths mostly not falling between the two means of the parents in the provinces (Fig. 7), but were longer than expected (Tab. 6). More specimens than expected also had earlier anthesis compared with the average anthesis development of the two parents, viz. 12 earlier and 6 later than expected (Fig. 7). This suggests that hybridization mainly involves long-spurred ecological races of *P. bifolia,* which in S Scandinavia also are the most early-flowering. Similarly, if the spur-length of the herbarium material from Öland is compared with the spur-lengths of intermediates on that island (field data), the latter are much longer than for the major part of the *P. bifolia* material (Fig. 7 right bottom diagram; *vide* also Nilsson 1983: Fig. 7).

Intermediates in extra-Nordic areas

Full information on this subject would require examination of all the thousands of "*P. bifolia*" and "*P. chlorantha*" sheets in the European herbaria, a scope beyond that of the present study. However, some general remarks can be made from the material studied and from other sources. Most comprehensive flora works mention records of hybrids, or intermediates, between *P. bifolia* and *P. chlorantha* in areas of sympatry (e.g. Ascherson & Graebner 1905–07, Camus & Camus 1928, Vermeulen 1958). Even if many of these records might be misidentifications, it is obvious that at least single hybrids are produced throughout the area of sympatry. Both material in this study (Tab. 7) and the literature

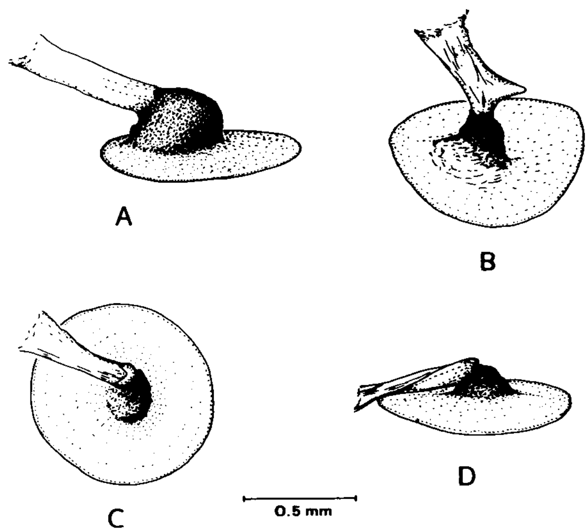
Fig. 7. Distribution of intermediates between *Platanthera bifolia* and *P. chlorantha* in the Nordic countries. The lateral diagrams represent pooled data on anthesis (week numbers indicated) and spur-length in *P. bifolia* (dotted line) and *P. chlorantha* (continuous line), and data on intermediate individuals. Hatched line in the Öland diagrams represents field data on intermediates, other data in the lateral diagrams are from herbarium material. Each spur-length distribution curve is based on measurements to the nearest mm and then conversion to per cent. Anthesis curves are based on % open flowers per week. Numbers for each curve are indicated (Pb: *P. bifolia*, Pc: *P. chlorantha*). – Symbols: dot = F_1-plant, square = $F_1 \times$ *P. chlorantha* (putative), star = $F_1 \times$ *P. bifolia* (putative).



Upl
Pb 151
Pc 96
Pb 257
Pc 137
Alandia
Pb 91
Pc 173
Pb 99
Pc 196
Ög,Nrk,
Sdm,Vstm
(cum.)
Pb 184
Pc 112
Pb 292
Pc 208
Gtl
Pb 58
Pc 60
Pb 86
Pc'101
Sm
Pb 45
Pc 86
Pb 112
Pc 139
Öld
Pb 46
Pc 76
F1 15
Pb 62
Pc 85
Interm. 89
MR
Pb 83
Pc 92
Pb 74
Pc 97
HO
Pb 178
Pc 274
Pb 193
Pc 286
Sk
Pb 99
Pc 133
Pb 193
Pc 222
Jutland
Pb 125
Pc 70
Pb 137
Pc 87
Zealand
Pb 60
Pc 35
Pb 82
Pc 58
100
%
Jun 25
30
20
mm
40

Tab. 3. Chemical composition of the floral fragrances of *Platanthera bifolia*, *P. chlorantha*, and a typical F_1-hybrid. For analytical conditions see text.

Compound	Quantity in fragrance (%; t trace). Relative quantity factor vs hybrid is given in parenthesis		
	P. bifolia	Hybrid	*P. chlorantha*
α-pinene	t	t	t
Sabinene	t	t	0.3
δ-3-carene	t	t	t
Myrcene	0.1	t	0.1
Limonene	0.3	t	t
β-ocimene – *cis*	0.1	t	t
β-ocimene – *trans*	5.7 (1.8)	7.4	t
Lilac alcohol	.	t	0.2
Benzaldehyde	t	1.1	0.6 (1.7)
Linalool	22.0	t	.
Lilac alcohol (M = 168)	.	16.3	46.1 (9)
Lilac alcohol (M = 168)	.	10.2	5.4 (1.7)
Lilac alcohol (M = 168)	.	2.7	9.1 (11)
Lilac alcohol (M = 168)	.	1.3	3.5 (9)
Trans-caryophyllene	0.3 (1.3)	0.6	0.5 (2.4)
Methylbenzoate	62.9 (17)	8.9	25.2 (9)
Neral	t	9.7	.
Lilac alcohol (M = 170)	.	0.8	0.6 (2.4)
Benzyl acetate	t	t	.
Geranial	t	13.9	.
Monoterpene alcohol	0.1 (0.8)	0.4	.
Methyl salicylate	2.3 (9)	0.6	0.1 (0.7)
Lilac alcohol (M = 170)	.	0.8	3.0 (12)
Nerol	t	3.2	.
Monoterpene alcohol	t	0.6	.
Lilac alcohol?	.	t	0.6
Geraniol	3.4 (1.2)	6.8	.
Benzyl alcohol	0.7 (0.2)	7.9	1.0 (0.4)
C_{14}-acid isopropylester	t	0.4	0.1 (0.7)
Cinnamic aldehyde	t	0.6	.
Cinnamyl acetate	0.1 (0.9)	0.3	.
Eugenol	0.2 (0.7)	0.6	.
Cinnamyl alcohol	0.6 (1.6)	0.9	.
Isoeugenol	0.6 (0.6)	2.3	.
Benzyl benzoate	0.6 (0.8)	1.8	3.6 (7)



Tab. 4. The occurrence of intermediates between *Platanthera bifolia* and *P. chlorantha* in the Nordic countries as indicated by the material in the herbaria.

Country & province	No. of specimens examined	Intermediates	
		No.	%
Norway	2981	4	0.13
Møre og Romsdal	196	3	1.53
Hordaland	534	1	0.19
Finland	1725	5	0.29
Alandia	316	5	1.58
Sweden	3227	27	0.84
Uppland	433	3	0.69
Västmanland	65	2	3.08
Södermanland	217	2	0.92
Närke	107	5	4.67
Östergötland	172	4	2.33
Gotland	209	4	1.91
Småland	277	4	1.44
Skåne	442	3	0.68
Denmark	600	3	0.50
Zealand	155	2	1.29
Jutland	264	1	0.38
The Nordic countries	8533	39	0.46

suggest that Atlantic regions of W Europe, and especially the British Isles (cf. Godfrey 1933, Hunt 1975), have less production of hybrids than continental areas such as Austria and Germany (and Sweden cf. above). Measurements indicated (Tab. 7) that also in C Europe hybrids mainly occur in areas where *P. bifolia* is represented by long-spurred, predominantly sphingid-pollinated races. In several cases material from Austria suggested presence of hybrid swarms. At a German locality Müller (1868) documented abundance of intermediates and obvious introgressive hybridization into a very long-spurred *P. bifolia* race.

Intermediates in extra-Nordic areas were not found to differ substantially in morphology from those in the Nordic area. An exception was a plant from the island of Corfu, Greece, which according to all essential details must be interpreted as a hybrid. It had, as expected, a caudicle ca. 0.6 mm long but, in addition, exhibited a very conspicuous pedicel, almost as in *P. chlorantha* (Fig. 8 A). However, even *P. bifolia* from Corfu was found to have a rather distinct pedicel (Fig. 8 B). This might reflect local pollination-race differentiation of *P. bifolia* on that island, perhaps under the influence

Fig. 8. Basal portion of the pollinaria in some extra-Nordic *Platanthera*. – A: Individual of hybrid origin, with large pedicel and caudicle ca. 0.60 mm long, from Corfu, Greece (Kalami; P. Lassen No. 4-1 (LD)). – B: *P. bifolia* from Corfu (M. Young No. 334/H (UPS)). Note the rather distinct pedicel. – C and D: *P. metabifolia* from Japan (Yego: Shari: J. Ohwi No. 4895 (UPS)), dorsal and lateral view. The pedicel is rather distinct and placed centrally on the suborbicular disc.

Tab. 5. Number of collected specimens, spur-length, and separation of anthesis of *Platanthera bifolia* and *P. chlorantha* in provinces of the Nordic countries. Based exclusively on material in the herbaria. Provinces with less than 10 collected individuals of either species have been excluded. Correlation coefficients (r) have been calculated for the number of intermediates (Tab. 4) versus each column of data. NS, not significant correlation.

Country & province	No. of plants			Mean spur-length (mm)			Separation at 50% anthesis (days)
	P. bifolia	*P. chlorantha*	Difference (%)	*P. bifolia*	*P. chlorantha*	Difference	
Norway							
Nord-Trøndelag	121	10	84.7	17.9	23.8	−5.9	–
Sør-Trøndelag	231	20	84.1	18.2	24.6	−6.4	4
Møre og Romsdal	87	106	− 9.8	19.9	24.3	−4.4	1
Sogn og Fjordane	191	190	0.26	22.1	24.4	−2.3	0
Hordaland	213	320	−20.1	23.4	24.6	−1.2	6
Rogaland	64	91	−17.4	20.7	23.9	−3.2	1
Vest-Agder	84	53	22.6	23.8	25.5	−1.7	6
Aust-Agder	34	28	9.7	25.5	26.9	−1.4	4
Telemark	73	17	62.2	26.9	30.0	−3.1	11
Vestfold	58	50	7.4	29.1	28.6	0.5	9
Buskerud	72	47	21.0	29.6	27.0	2.6	7
Akershus	69	173	−43.0	29.4	26.2	3.2	12
Østfold	66	15	63.0	25.9	28.3	−2.4	15
Finland							
Alandia	106	205	−31.8	24.1	22.2	1.9	13
Regio aboensis	250	72	55.3	28.7	22.4	6.3	11
Sweden							
Uppland	279	151	29.8	25.7	22.7	3.0	22
Södermanland	159	56	47.9	24.6	24.1	0.5	11
Vestmanland	40	23	27.0	25.3	24.8	0.5	14
Närke	45	57	−11.8	22.7	23.5	−0.8	6
Östergötland	88	80	4.8	23.1	24.4	−1.3	3
Dalsland	36	10	56.5	23.7	26.4	−2.7	–
Bohuslän	63	62	0.8	24.0	25.5	−1.5	14
Västergötland	139	240	−26.6	21.0	24.6	−3.5	1
Småland	122	151	−10.6	22.3	24.9	−2.9	3
Gotland	98	107	− 4.4	25.8	27.6	−1.8	14
Öland	71	93	−13.4	25.4	24.7	0.7	11
Halland	35	25	16.7	20.5	24.4	−3.9	10
Blekinge	72	52	16.1	22.0	24.9	−2.9	17
Skåne	203	236	− 7.5	22.0	24.2	−2.2	2
Denmark							
Zealand	92	61	20.3	20.7	25.1	−4.4	11
Jutland	167	96	27.0	20.6	24.5	−3.9	12
r	0.097	0.292	−0.350	−0.118	−0.434	0.102	−0.062
t_s	0.523	1.641	2.013	0.643	2.596	0.552	0.323
df	29	29	29	29	29	29	27
	NS	NS	NS	NS	$P<0.02$	NS	NS

of introgressive hybridization. *P. bifolia* examined from the Middle East, Iran, the Irkutsk area, and other parts of eastern USSR showed no tendency for developing a pedicel.

Remarks on Platanthera in E Asia

In east Asia, *P. bifolia* and *P. chlorantha* are replaced by related species with analogous pollination adaptations and thus similar floral morphologies (*vide* Inoue 1983b). In Manchuria, Sachalin, the Kurile Islands, and Japan a plant by the name of *P. metabifolia* Maek. occurs. This species is very similar to *P. bifolia* in habitus, and floral morphology and function. According to Inoue (1983b), the connective is narrow, ca. 0.7 mm wide, the caudicle of pollinia ca. 0.6 mm long, and the viscidia attach onto the base of the proboscis in *Deilephila* spp. (Sphingidae). Thus, the distance between the viscidia on the column must be small (the flower illustrated by Inoue has a distance of ca. 1.4 mm). Now, the column of *P. metabifolia* is extremely similar to that of the hybrid between *P. bifolia* and *P. chlorantha* characterized above. The viscidia are suborbicular and larger than in *P. bifolia*, the pedicel is distinctly developed, and also the length and structure of the caudicle (Fig. 8 C,D) is similar to that of the *Platanthera* intermediates from Europe.

Tab. 6. Spur-length of hybrids between *Platanthera bifolia* and *P. chlorantha* in the Nordic countries (herbarium material). The expected spur-length for F_1 is the mean of the means for *P. bifolia* and *P. chlorantha* in each province.

Country & province	Length of spur (mm)	Expected spur-length of F_1 (mm)	No. longer than expected	No. shorter than expected
Norway				
Møre og Romsdal	23.5, 24	22.1	2	.
Hordaland	27.5	24.0	1	.
Finland				
Alandia	20.5, 25, 25.5, 27.5, 29	23.2	4	1
Sweden				
Uppland	25, 25.5, 29.5	24.2	3	.
Södermanland	24, 25.5	24.4	1	1
Västmanland	22.5, 25	25.1	.	1
Närke	22.5, 23.5, 24.5, 25, 26	23.1	4	1
Östergötland	19.5, 27.5, 29	23.8	2	1
Småland	23, 23.5, 24, 24	23.6	2	1
Gotland	26, 26, 30	26.7	1	2
Skåne	24, 25, 27.5	23.1	3	.
Denmark				
Zealand	21	22.9	.	1
Jutland	32.5	22.6	1	.
			24	9

From a functional point of view, *P. metabifolia* and the hybrid *P. bifolia* × *P. chlorantha* are expected to be identical.

The question arises why a plant with such morphological structures can act as a separate species in E Asia while another, similar one, is strongly disfavoured by natural selection in other areas. Some specific morphological factor in the interaction with visiting moths in E Asia is the most plausible explanation. Alternatively, *P. metabifolia* seems to be either a result of directional selection from *P. bifolia* or a hybridogenic product which has undergone only some minor further adaptation in relation to the oriental pollination environment while becoming stabilized as a true species.

Tab. 7. Distribution, number, and spur-length of intermediates between *Platanthera bifolia* and *P. chlorantha* from extra-Nordic areas. Based on herbarium material.

Country	No. of plants examined	No. of intermediates	Length of spur in intermediates (mm)
Germany	129	7	20.5, 23, 29, 30.5, 30.5, 33, 38
Poland	29	1	22.5
Austria	140	6	24, 24.5, 28.5, 30, 32.5, 35.5
France	80	3	41.5, 42.5
Greece	53	2	18.5, 23.5
Turkey	28	2	24.5, 26
USSR	149	4	22, 24, 25.5, 31.5

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Appendix

List of records of intermediates between *Platanthera bifolia* and *P. chlorantha* in the Nordic countries.

F_1-hybrids

NORWAY, *Hordaland:* Tysnes, Slettaskog, 8 VII 1920 (J. Holmboe) (BG). *Möre og Romsdal:* Storfjorden, Vidhammer og Dyrhem, 8 VII 1918 (O. Dahl) (O); Storfjorden, Stordal, Dybdal, 21 VII 1962 (B. I. Grönningsäter) (BG).

FINLAND, *Alandia:* Eckerö, Storby, Käringsund, 30 VI 1954 (K. Pohjakallio) (H); Föglö, Jyddö, 6 VII 1907 (C. G. Tigerstedt) (H); Kökar, Karlbylandet W-part, W side of Kalen hill, 28 VI 1973 (U. Laine & J. Virtanen) (TUR); Jomala, Kråkör, 7 VII 1898 (A. L. Backman) (S); Lemland, Norrby, 1 VII 1919 (T. Putkonen) (H).

SWEDEN, *Skåne:* S Åsum, Sjöbo ora, June 1889 (G. Johansson) (S); Åspinge, 1.3 km ESE of church, 22 VII 1967 (A. Oredsson) (LD); Specimen without locality (v. Düben) (S). *Småland:* Åby, Björnö, parken, 15 VII 1927 (H. Bruun) (UME); Hultsjö, L. Kråkhult, 28 VI 1953 (F. Lundberg) (LD); Järstorp, between Klänestorp and Klockarp, July 1909 (S. Nordenstam) (S); Gränna, Långliden (C. J. Lindeberg) (GB). *Öland:* Sandby, between Ekelunda and Vället, 25 VI 1973; Gårdby, 1 km N of Ullevi*, several plants VI–VII 1974–82; Torslunda, Lenstad, 1 km N and 0.5 km E of Holmen*, several individuals VI–VII 1972–82; Torslunda, Tävelsrum, Tocknekärr, two plants 19 VI 1973 and one plant 25 VI 1982; Torslunda, Tävelsrum, 0.2 km W of Hildeborg*, several plants VI–VII 1973–82 (all records by L. A. Nilsson). *Gotland:* Othem, June 1891, two specimens (M. Östman) (S); Othem, Slite, 30 VI 1919 (T. Arvidsson) (S); Bäl, Kallgatskog, two plants 2 VII 1982; Fröjel, Mulde, one plant 7 VII 1982; Lummelunda, 2 km N of church, several plants VII 1982; Gothem, Gothemshammar 1 VII 1981; Hangvar, E of Träskmyr, two specimens 27 VI 1980 and one 6 VII 1982 (latter five records by L. A. Nilsson). *Östergötland:* V. Tollstad, Omberg, two specimens 5 VII 1950 (H. Smith) (UPS); Godegård, Godegård-Tjällmo 1 VII 1896 (A. P. Gustafsson) (LD). *Närke:* Örebro, Almby, towards Åskog, two specimens 5 VII 1932 (E. Broddeson) (S); Längbro, Vallby, two specimens, July 1924 (E. Broddeson) (S); Götlunda, Hästnäs, 10 VII 1948 (F. Fridell) (LD). *Södermanland:* Ornö, Mjöfjällsö, 4 VII 1933 (G. Samuelsson & E. Asplund) (S); Nämdö, Mörtöklubb, 8 VII 1931 (E. Asplund) (S). *Västmanland:* Kung Karl, Skillinge Norrgård, 1851 (UPS). *Uppland:* Värmdö, Fågelbro, 6 VII 1972 (E. Almquist) (UPS); Möja, Långviks Västerö, 12 VII 1923 (T. Vestergren) (S); Djurö, Runmarö, 11 VII 1919 (E. Nordström) (GB); Herräng, Häverö, Prästängen, 24 VI 1978 (L. A. Nilsson).

DENMARK, *East Jutland:* Stagsrode, Stagsevold Skov, v. Askemosen, 20 VI 1971 (B. Løjtnant) (AAU). *North East Zealand:* Distr. 45a+, label unreadable, 26 VI 1825 (Ch.) (C).

F_1 × P. bifolia (putative)

NORWAY, *Möre og Romsdal:* Norddal, Tobakken, Fjöra, 1 VII 1969 (B. I. Grönningsäter) (BG).

SWEDEN, *Öland:* Recorded from the localities above, marked with asterisks (L. A. Nilsson). *Gotland:* Hall, between Hall and Västös, 25 VI 1981; Lummelunda, 2 km N of church, one plant 30 VI 1981 and several plants VII 1982 (all records by L. A. Nilsson).

DENMARK, *South Zealand:* Basnæs skov, 3 VII 1872 (P. Nielsen) (GB).

F_1 × P. chlorantha (putative)

SWEDEN, *Öland:* Recorded from the localities above marked with asterisks (L. A. Nilsson). *Gotland:* Klinte, Klintehamn, 15 VII 1862 (G. F. Widgren) (UPS); Fröjel, at Hoxelmyr, 26 VI 1981; Hangvar, 1.5 km NW of church, 7 VII 1980 and E of Träskmyr 6 VII 1982; Lummelunda, ca. 2 km N of church, several plants 6 VII 1982; Hall, at Västös, two plants 7 VII 1980 (all records by L. A. Nilsson). *Östergötland:* V. Tollstad, Omberg 5 VII 1950 (H. Smith) (UPS).